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# ANALYSIS OF KNOWN AND NEW HOST RECORDS FOR *TRUPANEA* FROM CALIFORNIA (DIPTERA: TEPHRITIDAE)

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*Abstract.*—One hundred twenty-four, new rearing records are reported for eight of the 16 known species of *Trupanea* occurring in California. The host relations of all 16 species are assessed, including *T. texana* Malloch newly reported from California, for which hosts are unknown; one species for which only the host genus is known; four other monophagous species; three oligophagous species (one host tribe); one nearly oligophagous species; and six generalist species, all restricted to Asteraceae. *Trupanea signata* Foote is reported for the first time as a monophagous, obligate stem-gall former on *Gnaphalium luteo-album* L. One other monophagous species, as known to date, probably also is an obligate gall former; whereas, another is a facultative gall former. All other 11 species are ovule and soft achene feeders in flower heads, including *Trupanea arizonensis* Malloch, newly reported as monophagous on *Trixis californica* Kellogg. The host tribes are tabulated and the number of host genera and species within them are enumerated for each fly species. The six generalist species have been reared from at least five tribes each. This dispersed pattern of hosts among tribes is discussed in terms of procedures for determining the host specificities of Tephritidae as candidate agents for biological control of weeds. Two plant species, *Brickellia oblongifolia* Nuttall in the tribe Eupatorieae and *Haplopappus squarrosus* Hooker and Arnott in the tribe Astereae, are attacked by all six generalists. The Astereae, Cichorieae, Helenieae, Heliantheae, and Senecioneae contain the most host-plant genera and species recorded, and also are the largest of the 12 tribes of Asteraceae in southern California.

*Key Words:* Insecta, *Trupanea*, Tephritidae, Asteraceae, flower head-feeders, host specificities, monophagy, oligophagy, gall-formers, biological control, evolution, resource utilization, speciation

Six years ago I reported many new records for *Trupanea* (Diptera: Tephritidae) reared from flower heads of Asteraceae in southern California (Goeden 1985). This paper reports additional rearing records acquired since mid-1984 from both northern and southern California for this common and widespread genus of nonfrugivorous fruit flies (Foote and Blanc 1963).

## Materials and Methods

Materials and methods used were described by Goeden (1985). My earlier emphasis on sampling in southern California was changed during 1985–1990 to include collecting trips of 3- to 5-days duration to northern California, as floristically and geographically defined by Munz (1974). This expanded collecting effort in northern California allowed sampling of plant species and Tephritidae not present, or only of limited occurrence, in southern California (Munz and Keck 1959, Foote and Blanc 1963, Munz 1974). Voucher specimens of tephritids reside in my research collection; pressed voucher specimens of uncommon

or otherwise poorly represented host-plant species were deposited in the Herbarium of the University of California, Riverside. A sixteenth species in California, *Trupanea texana* Malloch, was identified in 1982 by F. L. Blanc (in litt. 1991) from one male collected by W. R. M. Mason at W. Palm Springs, Riverside Co., on 3.v.1955. This specimen was deposited in the Canadian National Collection at Ottawa, Canada.

## Results

New rearing records are listed below for eight of 15 species of *Trupanea* reported from California by Foote and Blanc (1963). Host records unreported by Wasbauer (1972), Cavender and Goeden (1982, 1983), Goeden (1985, 1986, 1987, 1988), and Headrick and Goeden (1991) are listed by genera and species in a slightly different, more readible manner from Goeden (1985). Unless otherwise noted, all flies were reared from ca. 1-liter samples of mature flower heads. Among multiple samples of a particular new host-plant species, only the sample from which the most individuals of each fly species was recovered is reported. The plant nomenclature used largely follows Munz and Keck (1959) and Munz (1968, 1974); the insect nomenclature follows Foote (1960) and Foote and Blanc (1963). Rearing records for the flies and their host plants are listed alphabetically.

### *Trupanea actinobola* (Loew)

*New host genera: Amphipappus, Brickellia, Haplopappus, Trichoptilium.*

*New host records: Amphipappus fremontii* Torrey and Gray; 1 ♂ and 1 ♀; Wheeler Canyon at 1204 m, Inyo Nat. Forest, Inyo Co.; 21.v.1988. *Aster spinosus* Bentham; 5 ♂ and 3 ♀; NW of Blythe at 85 m, Riverside Co., 2.xii.1987. *Bailyea pleniradiata* Harvey and Gray; 3 ♂ and 6 ♀; sand dunes NW of Indio at Hidden Springs, Riverside Co.; 14.iv. 1986. *Brickellia oblongifolia* Nuttall; 3 ♂; Santa Rosa Mountain at about 1400 m, San Bernardino Nat. Forest (S section), Riverside Co.; 14.vi.1988. *Gutierrezia bracteata* Abrams; 2 ♂ and 4 ♀; Bratton Valley at 387 m, San Diego Co.; 31.v.1989. *Gutierrezia sarothrae* (Pursh) Britton and Rusby; 18 ♂ and 9 ♀; Mountain Springs, SW Imperial Co; 6.xi.1986. *Haplopappus bloomeri* Gray; 1 ♂; Beasore Meadow at 1972 m, Sierra Nat. Forest, Sierra Co.; 16.viii.1988. *Haplopappus cooperi* (Gray) Hall; 4 ♂ and 2 ♀; Mojave River Forks, San Bernardino Nat. Forest, SW San Bernardino Co.; 12.v.1987. *Haplopappus squarrosus* Hooker and Arnott; 3 ♂ and 1 ♀; Kitchen Creek Road above Cibbetts Flat Campground at 1341 m, Cleveland Nat. Forest, San Diego Co.; 6.x.1988. *Trichoptilium incisum* (Gray) Gray; 3 ♀; Indian Well, Imperial Co.; 12.iii.1986.

### *Trupanea femoralis* (Thomson)

*New host genera: Baccharis, Brickellia, Eriophyllum, Holocarpa, Lessingia, Machaeranthera, Monolopia, Perezia, Viguiera.*

*New host records: Baccharis salicifolia* (Ruiz and Pavon) Persoon (= *glutinosa* Persoon); 1 ♂ and 1 ♀; bottom of Parkfield-Coalinga Grade near San Andreas Fault at 393 m, Fresno Co.; 18.iv.1989. *Brickellia oblongifolia*; 5 ♂ and 2 ♀; base of Santa Rosa Mountain, San Bernardino Nat. Forest (S section), Riverside Co.; 14.vi.1988. *Chrysothamnus paniculatus* (Gray) Hall; 1 ♂; N of Pioneertown atop N rim of Chaparossa Wash at 1356 m, SW San Bernardino Co.; 31.x.1990. *Chrysothamnus teretifolius* (Durand and Hilgard) Hall; 2 ♂; along Death Valley Road as it leaves Owens Valley at 1378 m, Inyo Co.; 11.x.1990. *Eriophyllum lanatum* (Pursh) Forbes; 1 ♂ and 1 ♀; Cedar Slope along State Highway 190 at 1646 m, Sequoia Nat. Forest, Tulare Co.; 12.vi.1990. *Haplopappus cuneatus* Gray; 2 ♂ and 1 ♀; Alder Saddle, S of Pacifica Mountain at 1737 m, Angeles Nat. Forest, Los Angeles Co.; 20.ix.1990. *Haplopappus lanceolatus* (Hooker) Torrey and Gray; 1 ♂; open meadow on N shore of Frenchman Lake at 1703 m, Plumas Nat. Forest, Plumas Co.;

22.viii.1989. *Haplopappus propinquus* Blake; 1 ♂; Mountain Springs Pass, SE San Diego Co.; 7.x.1987. *Haplopappus racemosus* (Nuttall) Torrey; 1 ♀; saline, grassy meadow in Fish Slough, 10 km N of Bishop at 1225 m, Inyo Co.; 9.x.1990. *Hemizonia kelloggii* Greene; 1 ♂; Valle Vista at 546 m, Riverside Co.; 1.vii.1988. *Holocarpa heermannii* (deCandolle) Greene; 10 ♂ and 5 ♀; Tule River Indian Reservation above S Fork of Tule River at 438 m, Tulare Co.; 17.v.1989. *Holocarpa virgata* (Gray) Keck; 4 ♂ and 7 ♀; E of Sacramento off State Highway 50 at 128 m, Sacramento Co.; 7.ix.1987. *Lessingia glandulifera* Gray; 1 ♂ and 1 ♀; dry bed of Hamilton Creek, E of Anza at 1222 m, Riverside Co.; 28.ix.1989. *Lessingia lemmonii* Gray; 1 ♂; Big Meadow, S of Tom's Place above Round Valley at 1966 m, Mono Co.; 10.x.1990. *Lessingia nemaclada* Greene; 1 ♂ and 1 ♀; Big Sandy Bluff along State Highway 168 at 1280 m, Sierra Nat. Forest, Fresno Co.; 17.viii.1988. *Machaeranthera tephrodes* (Gray) Greene; 1 ♂ and 1 ♀; W end of Jacumba at 866 m, San Diego Co.; 6.xi.1986. *Monolopia lanceolata* Nuttall; 35 ♂ and 39 ♀; Tremlor Range, along State Highway 58, E of California Valley, San Luis Obispo Co.; 10.iv.1987. *Perezia microcephala* (deCandolle) Gray; 2 ♀; mouth of Mill Creek Canyon at 1200 m, San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 6.vii.1989. *Viguiera laciniata* Gray; 2 ♀; 5 km S of Alpine at 460 m, San Diego Co.; 18.iv.1989.

*Trupanea jonesi* Curran

*New host genera: Achrachaena, Antennaria, Aster, Blepharipappus, Brickellia, Chrysopsis, Hulsea, Lasthenia, Madia, Monolopia.*

*New host records: Achrachaena mollis* Schauer; 10 ♂ and 12 ♀; S of Camp Roberts Military Reservation, near Chimney Rock, San Luis Obispo Co.; 19.iv.1988. *Antennaria rosea* Greene; 1 ♂ and 1 ♀; along Deadman Creek at 2408 m, Inyo Nat. Forest, Mono Co.; 21.vii.1987. *Arnica longifolia* deCandolle; 34 ♂ and 27 ♀; Deadman Creek, W of Sonora Pass at 2790 m, Stanilaus Nat. Forest, Tuolumne Co.; 8.ix.1988. *Arnica sororia* Greene; 16 ♂ and 26 ♀; along Deadman Creek at 2499 m, Inyo Nat. Forest, Mono Co; 9.ix.1986. *Artemisia cana* Pursh; 1 ♀; Campito Meadow on White Mountain at 3246 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Artemisia michauxiana* Besser; 1 ♂; below Patriarch Grove on White Mountain at 3414 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Aster alpigenus* (Torrey and Gray) Gray; 7 ♂ and 13 ♀; Kaiser Pass Meadow at 2720 m, Sierra Nat. Forest, Fresno Co.; 17.viii.1988. *Aster campestris* Nuttall; 3 ♂ and 1 ♀; E side of Frenchman Lake at 1728 m, Plumas Nat. Forest, Plumas Co.; 22.viii.1989. *Aster eatonii* (Gray) Howell; 15 ♂ and 18 ♀, above Perazo Meadow, Tahoe Nat. Forest, Sierra Co.; 10.ix.1986. *Aster integrifolius* Nuttall; 36 ♂ and 34 ♀; Jackass Meadow at 2256 m, Sequoia Nat. Forest, Tulare Co.; 24.vii.1984. *Aster occidentalis* (Nuttall) Torrey and Gray; 21 ♂ and 23 ♀; W of Sonora Pass at 2850 m, Stanilaus Nat. Forest, Tuolumne Co.; 8.ix.1988. *Blepharipappus scaber* Hooker; 1 ♂; W of Fandango Pass at 1615 m, Modoc Nat. Forest, Modoc Co.; 23.viii.1989. *Brickellia oblongifolia*; 2 ♀; Waucoba Canyon, Inyo Nat. Forest, Inyo Co.; 10.vi.1987. *Chaenactis glabriuscula* deCandolle; 9 ♂ and 9 ♀; junction of La Panza Road and State Highway 58 at 433 m, San Luis Obispo Co.; 18.iv.1990. *Chaenactis parishii* Gray; 1 ♂ and 2 ♀; Santa Rosa Mountain at 1554 m, San Bernardino Nat. Forest (S section), Riverside Co.; 3.vi.1987. *Chaenactis santolinoides* Greene; 1 ♂ and 1 ♀; Burnt Peak, Angeles Nat. Forest, Los Angeles Co.; 28.v.1988. *Chaenactis steviodes* Hooker and Arnott; 7 ♂ and 9 ♀; Walker Well, N side of Freeman Canyon, E of Walker Pass, Kern Co.; 8.v.1990. *Chaenactis xantiana* Gray; 40 ♂ and 29 ♀; Shell Creek Road, Avenales Wildlife Area at 390 m, San Luis Obispo Co.; 18.iv.1990. *Chrysopsis breweri* Gray; 1 ♂ and 2 ♀; NE of Shaver Lake at 2170 m,

Sierra Nat. Forest, Fresno Co.; 17.viii.1988. *Coreopsis bigelovii* (Gray) Hall; 1 ♂ and 3 ♀; N side of Yucca Valley at 1173 m, SW San Bernardino Co.; 16.iii.1988. *Eriophyllum ambiguum* (Gray) Gray; 4 ♂ and 4 ♀; Spanish Needle Creek, S of Lamont Peak at 1250 m, Kern Co.; 11.iv.1989. *Eriophyllum lanatum*; 4 ♂ and 5 ♀; Deadman Creek, along Deadman Creek at 2499 m, Inyo Nat. Forest, Mono Co.; 21.vii.1987. *Haplopappus acaulis* (Nuttall) Gray; 7 ♂ and 5 ♀; N of Crooked Creek, White Mountain at 3173 m, Inyo Nat. Forest, Mono Co.; 26.vii.1989. *Haplopappus apargioides* Gray; 2 ♂; Poison Creek on White Mountain at 3155 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Haplopappus bloomeri*; 8 ♂ and 4 ♀; Niagra Creek Campground at 1900 m, Stanilaus Nat. Forest, Tuolumne Co.; 8.ix.1988. *Haplopappus cooperi* (Gray) Hall; 1 ♂ and 1 ♀; Walker Well, N side Freeman Canyon, E of Walker Pass, Kern Co.; 8.v.1990. *Haplopappus lanceolatus* (Hooker) Torrey and Gray; 5 ♂ and 6 ♀; meadow on shore of Frenchman Lake at 1704 m, Plumas Nat. Forest, Plumas Co.; 22.viii.1989. *Haplopappus macronema* Gray; 1 ♂ and 4 ♀; Deadman Creek, W of Sonora Pass at 2790 m, Stanilaus Nat. Forest, Tuolumne Co.; 8.viii.1988. *Haplopappus suffruticosus* (Nuttall) Gray; 2 ♂ and 6 ♀; County Line Hill on White Mountain at 3170 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Hulsea vestita* Gray; 2 ♂; rocky scree near Big Meadow at 2286 m, Sequoia Nat. Forest, Tulare Co.; 12.vi.1985. *Lasthenia californica* deCandolle ex Lindley; 2 ♂; Figueroa Mountain at 792 m, Los Padres Nat. Forest, Santa Barbara Co.; 17.iv.1985. *Lasthenia glabrata* Lindley; 1 ♂; San Jacinto Valley, Riverside Co.; 3.vi.1987. *Layia ziegleri* Munz; 1 ♂ and 3 ♀; Junction of State Highways 74 and 371, Burnt Valley at 1372 m, San Bernardino Nat. Forest (S section), Riverside Co.; 12.v.1988. *Madia gracilis* (Smith) Keck; 3 ♀; Silver Lake at 2195 m, Inyo Nat. Forest, Mono Co.; 21.vii.1987. *Monolopia lanceolata*; 1 ♂; Tremlor Range, along State Highway 58, E of California Valley, San Luis Obispo Co.; 10.iv.1987. *Senecio breweri* Davy; 4 ♂ and 2 ♀; Doney, S of Woody at 1006 m, Kern Co.; 18.v.1989. *Senecio integerrimus* Nuttall; 6 ♂ and 5 ♀; S of Patriarch Grove, White Mountain at 3149 m, Inyo Nat. Forest, Mono Co.; 26.vii.1989. *Senecio multilobatus* Torrey and Gray; 4 ♂ and 9 ♀; White Mountain at 3048 m, Inyo Nat. Forest, Inyo Co.; 18.vi.1986. *Senecio serra* Hooker; 1 ♂; June Lake at 2316 m, Inyo Nat. Forest, Mono Co.; 21.vi.1987. *Senecio triangularis* Hooker; 10 ♂ and 6 ♀; Dana Plateau on White Mountain at 3353 m, Inyo Nat. Forest, Mono Co.; 8.viii.1986. *Solidago californica* Nuttall; 1 ♂ and 1 ♀; 4.8 km W of Hat Creek, Lassen Nat. Forest, Shasta Co.; 24.viii.1989. *Solidago canadensis* L.; 2 ♂ and 5 ♀; along Deadman Creek at 2499 m, Inyo Nat. Forest, Mono Co.; 9.ix.1986. *Solidago multiradiata* Aiton; 3 ♂; Horseshoe Meadow at 2926 m, Inyo Nat. Forest, Inyo Co.; 22.vii.1987.

*Trupanea nigricornis* (Coquillett)

*New host genera: Amphipappus, Dicoria, Geraea, Madia, Monolopia.*

*New host records: Amphipappus fremontii* Torrey and Gray; 1 ♂; Wheeler Canyon at 1204 m, Inyo Nat. Forest, Inyo Co.; 21.v.1988. *Baccharis sarathroides* Gray; 1 ♂; Proctor Valley at 168 m, SW San Diego Co.; 8.x.1987. *Chrysothamnus albidus* (Jones) Greene; 1 ♂ and 1 ♀; Fish Slough, N of Bishop at 1286 m, Inyo Co.; 21.viii.1989. *Chrysothamnus parryi* (Gray); 2 ♂; above Jackass Meadow, Sequoia Nat. Forest, Tulare Co.; 24.vii.1984. *Dicoria canescens* Torrey and Gray; 2 ♂ and 1 ♀; sand dunes at Glamis, Imperial Co.; 5.xi.1986. *Eriophyllum lanatum*; 1 ♂; Crowder Flat at 1542 m, Modoc Nat. Forest, Modoc Co.; 23.viii.1989. *Geraea viscida* (Gray) Blake; 4 ♂ and 7 ♀; Kitchen Creek Canyon, Cleveland Nat. Forest, San Diego Co.; 27.iv.1985. *Haplopappus bloomeri* Gray; 6 ♂ and 4 ♀; Beasore Meadow at 1970 m, Sierra Nat. Forest, Madera Co.; 16.viii.1988. *Haplopappus linearifolius* deCandolle; 1 ♂; along

Sherman Pass Road above N Meadow Creek at 1585 m, Sequoia Nat. Forest, Tulare Co.; 21.v.1986. *Haplopappus propinquus* Blake; 1 ♀; Mountain Springs Pass, Inyo Co.; 7.x.1987. *Haplopappus squarrosus*; 1 ♂; Kitchen Creek Canyon, Cleveland Nat. Forest, San Diego Co.; 23.x.1985. *Haplopappus suffruticosus* (Nuttall) Gray; 1 ♂; County Line Hill, White Mountain at 3170 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Iva axillaris* Pursh; 1 ♀; NW of Chimney Peak, Sequoia Nat. Forest, Tulare Co.; 30.vii.1986. *Machaeranthera tortifolia* (Gray) Cronquist and Keck; 6 ♂ and 6 ♀; Death Valley Road, Last Chance Mountain Range at 975 m, Inyo Co.; 9.vi.1987. *Perezia microcephala*; 7 ♂ and 4 ♀; Mill Creek Canyon at 1250 m, San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 28.vii.1990. *Psathyrotes annua* (Nuttall) Gray; 1 ♂ and 1 ♀; Fish Slough, N of Bishop at 1314 m, Mono Co.; 25.vii.1990. *Psathyrotes ramosissima* (Torrey) Gray; 1 ♂ and 5 ♀; Painted Canyon, Riverside Co.; 28.xi.1984. *Tetradymia glabrata* Gray; 71 ♂ and 62 ♀; Payson Canyon at 1707 m, Inyo Co.; 18.vi.1986. *Viguiera lacinata*; 2 ♀; W of Barrett Junction, N of Tecate Peak at 335 m, San Diego Co.; 4.iii.1988. *Viguiera reticulata* Watson; 12 ♂ and 11 ♀; Death Valley Road, base of Last Chance Mountain at 1128 m, Inyo Co.; 17.vi.1986.

*Trupanea radifera* (Coquillett)

*New host genera: Atrichoseris, Brickellia, Calycoseris, Dyssodia, Erigeron, Haplopappus, Lasthenia.*

*New host records: Atrichoseris platyphylla* Gray; 4 ♂ and 7 ♀; Death Valley Road at 835 m, N of Death Valley Nat. Monument, Inyo Co.; 18.v.1988. *Brickellia oblongifolia*; 2 ♀; Santa Rosa Mountain at 1402 m, San Bernardino Nat. Forest (S section), Riverside Co.; 3.vi.1987. *Calycoseris wrightii* Gray; 1 ♂ and 1 ♀; Death Valley Road, Last Chance Range at 178 m, Inyo Co.; 9.vi.1987. *Dyssodia cooperi* Gray; 1 ♂ and 2 ♀; Kane Springs, NE of Barstow near Rodman Mountains, W San Bernardino Co.; 4.v.1988. *Erigeron aphanactis* (Gray) Greene; 1 ♂; Hanging Rock Canyon, Last Chance Range at 1554 m, Inyo Co.; 17.vi.1986. *Eriophyllum lanosum* (Gray) Gray; 12 ♂ and 13 ♀; Lobeck's Pass, E San Bernardino Co.; 24.iii.1988. *Haplopappus apargioides*; 2 ♂ and 4 ♀; Poison Creek on White Mountain at 3155 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Haplopappus squarrosus*; 1 ♀; Poison Creek on White Mountain at 3246 m, Inyo Nat. Forest, Mono Co.; 19.viii.1987. *Lasthenia californica* deCandolle; 2 ♂ and 4 ♀; Warner Springs, San Diego Co.; 30.iv.1986. *Malacothrix saxatilis* (Nuttall) Torrey and Gray; 10 ♂ and 10 ♀; Mill Creek Canyon at 1230 m, San Bernardino Nat. Forest, SW San Bernardino Co.; 5.vi.1987. *Malacothrix sonchoides* (Nuttall) Torrey and Gray; 18 ♂ and 16 ♀; Death Valley Road at 853 m, N of Death Valley Nat. Monument, Inyo Co.; 18.v.1988. *Microseris campestris* Greene; 8 ♂ and 3 ♀; E of Pozo in Frazer Canyon at 500 m, Los Padres Nat. Forest, San Luis Obispo Co.; 17.iv.1990. *Microseris douglasii* (deCandolle) Schultz; 2 ♀; N of Parkfield, S of summit at 686 m, Monterey Co.; 18.iv. 1989. *Senecio breweri*; 1 ♂; E of Lake San Antonio at 344 m, Monterey Co.; 20.iv.1989. *Senecio multilobatus*; 4 ♂ and 4 ♀; White Mountain at 3048 m, Inyo Nat. Forest, Inyo Co.; 29.vii.1986.

*Trupanea signata* Foote

*New host record: Gnaphalium luteo-album* L.; 4 ♂ and 2 ♀ (reared from puparia dissected from galls on branches and stems of); N of Lake Hemet, Riverside Co.; 29.ix.1989.

*Trupanea vicina* (van der Wulp)

*New host genus: Pectis.*

*New host record: Pectis papposa* Harvey and Gray ex Gray; 1 ♂; just N of Signal Mountain, Imperial Co.; 29.xi.1984.

*Trupanea wheeleri* Curran

*New host genera: Baccharis, Brickellia, Helianthus, Perezia.*

*New host records: Baccharis plummerae* Gray Canada de Media; 2 ♂ and 1 ♀; Santa Cruz Island, Santa Barbara Co.; 7.x.1985. *Baccharis sarathroides*; 1 ♀; Proctor Valley at 168 m, SW San Diego Co.; 8.x.1987. *Brickellia oblongifolia*; 2 ♂ and 4 ♀; Santa Rosa Mountain at about 1400 m, San Bernardino Nat. Forest (S section), Riverside Co.; 14.vi.1988. *Chaenactis artemisiaefolia* (Harvey and Gray) Gray; 14 ♂ and 14 ♀; Aguanga Mountain at 1128 m, Cleveland Nat. Forest, San Diego Co.; 5.vi.1985. *Chrysothamnus teretifolius*; 15 ♂ and 19 ♀; Mountain Springs at 700 m, SW Imperial Co.; 6.xi.1986. *Haplopappus acradenius* (Greene) Blake; 2 ♂ and 2 ♀; Mountain Springs at 699 m, SW Imperial Co.; 6.xi.1986. *Haplopappus detonsus* (Greene) Raven; 1 ♀; Prisoners' Harbor, Santa Cruz Island, Santa Barbara Co.; 13.ix.1984. *Haplopappus linearifolius*; 1 ♀; Mill Creek Canyon at 1219 m, San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 8.v.1987. *Haplopappus palmeri* Gray; 34 ♂ and 27 ♀; N of Barrett Junction at 305 m, San Diego Co.; 20.x.1987. *Helianthus gracilentus* Gray; 5 ♂ and 5 ♀; San Ysidro, SW San Diego Co.; 10.iv.1987. *Hemizonia fasciculata* (deCandolle) Torrey and Gray; 8 ♀; Otay Mesa at 168 m, above San Ysidro, SW San Diego Co.; 31.v.1989. *Perezia microcephala*; 146 ♂ and 143 ♀; mouth of Mill Creek Canyon at 1200 m, San Bernardino Nat. Forest (N section), SW San Bernardino Co.; 28.vi.1989. *Solidago occidentalis* (Nuttall) Torrey and Gray; 1 ♂ and 2 ♀; Carpenteria, Santa Barbara Co.; 4.x.1987.

## Discussion

The host-plant specificities of *Trupanea* species reported from California after 11 years of field study remain largely as I initially assessed them (Goeden 1985), with a few noteworthy exceptions. *Trupanea pseudovicina* Hering continues to be assessed as a strictly monophagous species (Goeden 1985). *Trupanea arizonensis* Malloch reared from flower heads of *Trixis californicus* Kellogg was misidentified by me as *Trupanea actinobola* in Goeden (1985); although, the latter species also has been identified by F. L. Blanc (in litt. 1991) among other specimens that I reared from heads of this same host plant from the same location. I still have not reared *T. maculigera* Foote or *T. texana*; although, another rare species for which no host was known, *T. signata,* has since been reared, as reported above. *Trupanea signata* is now known to be a monophagous or nearly monophagous, obligate gall former, and its biology and ecology currently are under study in southern California (Goeden, Headrick, and Teerink, unpublished data). This discovery lent credence to the rearing record for *T. maculigera* from "galls in *Gnaphalium* sp." in Foote (1960), a reported mode of development on which neither he nor Wasbauer (1972) commented, perhaps because it may have been suspect at that time for any *Trupanea*. However, since then, Goeden (1987) reported facultative gall formation by *T. conjuncta* (Adams), and in the present paper, obligate gall formation by *T. signata.* Thus, it is quite probable that *T. maculigera* is indeed an obligate gall former on a still to be determined species of *Gnaphalium* (Foote 1960). Unfortunately, the rearing record from 1950 in Foote (1960) is from San Ysidro, California, just north of the border at Tijuana, Mexico, and presently this is a highly disturbed and otherwise problematic area in which to collect. Nevertheless, I am now in active pursuit of this tephritid in less disturbed, undeveloped areas along the border to the east in southcentral San Diego County.

The following species remain classed as oligophagous species (known from one host tribe, Goeden 1985): *T. bisetosa* (Coquillett), now known from four genera and six species of hosts, all in the tribe Heliantheae

Table 1. Numbers of host genera and species (tabulated as genera/species) for 16 species of *Trupanea* reported from nine tribes of Asteraceae in California.

| | Tribes | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Trupanea* sp. | Anthemideae | Astereae | Cichorieae | Eupatorieae | Helenieae | Heliantheae | Inuleae | Murtiseae | Senecioneae | Totals |
| *actinobola* | 1/1 | 8/14 | — | 1/1 | 4/5 | 1/1 | — | 1/1 | 1/1 | 17/24 |
| *arizonensis* | — | — | — | — | — | — | — | 1/1 | — | 1/1 |
| *bisetosa* | — | — | — | — | — | 4/6 | — | — | — | 4/6 |
| *californica* | — | — | — | — | — | — | 2/9 | — | — | 2/9 |
| *conjuncta* | — | — | — | — | — | — | — | 1/1 | — | 1/1 |
| *femoralis* | — | 9/22 | — | 1/1 | 2/2 | 3/6 | — | 1/1 | 2/2 | 18/34 |
| *imperfecta* | — | — | — | — | — | 3/3 | — | — | — | 3/3 |
| *jonesi* | 1/5 | 9/31 | 2/2 | 1/1 | 8/19 | 9/13 | 2/2 | — | 5/13 | 37/86 |
| *maculigera* | — | — | — | — | — | — | 1/1 | — | — | 1/1 |
| *nigricornis* | — | 10/28 | — | 2/6 | 3/3 | 6/12 | — | 1/1 | 5/9 | 27/59 |
| *pseudovicina* | — | — | — | — | 1/1 | 1/1[a] | — | — | — | 2/2 |
| *radifera* | — | 8/10 | 5/11 | 2/2 | 7/8 | 1/1 | — | — | 1/3 | 24/35 |
| *signata* | — | — | — | — | — | — | 2/2 | — | — | 2/2 |
| *texana* | — | — | — | — | — | — | — | — | — | — |
| *vicina* | — | — | — | — | 4/4 | 1/1 | — | — | — | 5/5 |
| *wheeleri* | — | 6/19 | — | 1/2 | 3/3 | 3/5 | — | 1/1 | — | 14/30 |

[a] The host record represented here for *Bebbia juncea* (Bentham) Greene in Wasbauer (1972) is probably erroneous (Goeden 1985, 1988, Goeden and Ricker 1989).

(Cavender and Goeden 1983, Table 1); *T. californica* Malloch, now known from two genera and nine species of hosts, all in the tribe Inuleae (Headrick and Goeden 1991, Table 1); and *T. imperfecta* (Coquillett), still known from three genera and three species, all in the tribe Astereae (Goeden 1988, Table 1).

*Trupanea vicina* (van der Wulp) is now assessed as nearly oligophagous (Goeden 1985). It is now known from five host species in five genera, four of which are in the tribe Helenieae, with a fifth host in the tribe Heliantheae (Table 1). This occasional pest of ornamental marigolds, *Tagetes* sp., recently also was selected for field and laboratory study in southern California.

The diversity of host plants attacked by each of the six species designated as generalists by Goeden (1985) was made even more apparent by the many new records presented in the present paper. Each of the following generalists is now known to infest hosts from at least five tribes of Asteraceae (Table 1), but only from this plant family, which thus serves to distinguish them from polyphages by my definition (Goeden 1985).

*Trupanea actinobola* is now known from nine tribes, 22 genera, and 38 species of Asteraceae in North America (Wasbauer 1972, Goeden 1985, and the present study). Twenty-four (63%) of its known hosts are from California (Table 1), and all but two of these represent my rearing records. One host species was reported by Wasbauer (1972) from each of the tribes Cichorieae and Inuleae, although I have not reared this fly from either tribe (Table 1). The majority of its hosts are in the tribes Astereae and Helenieae in California (Table 1).

*Trupanea femoralis* is now known from six tribes, 18 genera, and 34 species of Asteraceae in North America (Wasbauer 1972, Goeden 1985, 1986, and the present study). All 34 of its known hosts occur in California, and all but seven of these represent my rearing records. The majority of its hosts in California also are Asteraceae (Table 1).

*Trupanea jonesi* now has the broadest host range in terms of known genera and species

attacked of any native tephritid from California, indeed, probably from North America (Wasbauer 1972, Goeden 1985). As reported to date, its host range comprises eight tribes, 37 genera, and 86 species of Astereae in North America (Wasbauer 1972, Goeden 1985, and the present study). Only *T. actinobola* is known from more tribes, though fewer genera and species (see above). All 86 of the known hosts of *T. jonesi* are from California, and all but 13 of these represent my rearing records, including two from Wasbauer (1972) which I have confirmed. Again, most hosts of *T. jonesi* in California belong to the Astereae, with good representation also in the tribes Helenieae, Heliantheae, and Senecioneae (Table 1).

*Trupanea nigricornis* was one of the first generalists in this genus to have its biology studied in some detail (Cavender and Goeden 1983). It is currently under even more detailed study in southern California (Knio and Goeden, unpublished data), in comparison with its cryptic, sympatric, oligophagous congener, *T. bisetosa,* previously studied by Cavender and Goeden (1982). The known host range of *T. nigricornis* comprises seven tribes, 28 genera, and 60 species of Asteraceae (Wasbauer 1972, Cavender and Goeden 1983, Goeden 1985, and the present paper). All 60 hosts are from California, 55 of which represent my host records (Table 1). I have not confirmed five records in Wasbauer (1972), one of which, for *Carthamus tinctorius* L. in the tribe Cynareae is highly suspect in my opinion, and therefore, was not listed in Table 1. *Trupanea nigricornis* is otherwise unknown from thistles in the tribe Cynareae, the insect fauna and ecology of several native and introduced species of which have been studied in southern California for many years by my co-workers and me (c.f. Goeden and Ricker 1986, 1987). Moreover, no *Trupanea* species otherwise has been reared from Cynareae in California (Goeden and Ricker 1986, 1987; Table 1) or elsewhere in North America (Wasbauer 1972).

*Trupanea radifera* is now known from five tribes, 24 genera, and 35 species of Asteraceae in North America (Wasbauer 1972, Goeden 1985, and the present study). All but one host species occur in California (Table 1), and all but two hosts represent my rearing records. Most hosts of this tephritid belong to the tribes Cichorieae, Eupatorieae, and Helenieae (Table 1).

*Trupanea wheeleri* is now known from five tribes, 14 genera, and 29 species of host plants in North America (Wasbauer 1972, Goeden 1985, and the present study). All of its known hosts are from California and represent my rearing records. The majority of its hosts belong to the Astereae (Table 1).

I have stressed the contribution of California Asteraceae to knowledge of the hosts of these species of *Trupanea* in order to demonstrate how little is known about the host plants of these species elsewhere in North America. Only *T. maculigera* among them is known solely from California (Foote and Blanc 1963, F. L. Blanc in litt. 1991). Most other species of *Trupanea* occur in several western states; some, like *T. actinobola,* are distributed across North America (Foote 1960). Thus, this lack of knowledge of hosts, let alone biologies, involves one of the largest, most common, and widespread genera of nonfrugivorous Tephritidae native to the western United States (Foote 1960, Foote and Blanc 1963, Blanc and Foote 1987). The amount of fundamental data still to be obtained on the hosts of these and other nonfrugivorous Tephritidae is truely awesome.

The data in Table 1 for the six oligophagous species also demonstrate that their hosts are not limited to one or two favored tribes of Asteraceae, but rather may also involve scattering of only one or two hosts in each of several other tribes. Whether the flies on these few taxonomically isolated hosts in less well exploited tribes represent evolutionarily younger relationships resulting from host-plant transfers from one of the better utilized host tribes is an intriguing

question. Or are these relationships the vestiges of formerly, more heavily utilized tribes? The low numbers of flies reared from some host species indicate that those hosts were less suitable than others for reproduction (Goeden 1985). Thus, the question arises as to what drives these host transfers? Is it tephritid competition for natural enemy-free space (Price et al. 1980, Zwölfer 1982, Strong et al. 1984)? Or positive behavioral responses to similar flower head morphology (Zwölfer 1982, 1988)? Or, to similar host-plant architecture (Strong et al. 1984)? Or, perhaps, some or all of these factors, and more? And, from which taxa did their ancestors transfer? Presumably each transfer would involve biochemically closely related host taxa (Erlich and Raven 1964, Zwölfer 1987, 1988, Futuyma and McCafferty 1990).

The hosts of the generalist species represented in Table 1 are not clustered in one or two tribes, as one might expect from intra-tribal host shifts among closely related hosts. Nor are they clustered in only a few genera within the more heavily exploited tribes (Table 1). It would appear that the life strategies of these generalists is to "spread the risk" by reproducing on a wide range of hosts (Zwölfer 1983), or to specialize in not specializing (Moran and Southwood 1982).

*Trupanea californica, T. maculigera,* or *T. signata* may represent the products of a past, intertribal host-transfer by a facultative gall-forming, flower-head infesting ancestor like *T. conjuncta* (Goeden 1987) to the Inuleae, and the subsequent separation and speciation of its descendants as an obligate flower head-infesting species like *T. californica* (Headrick and Goeden 1991), and obligate gall-formers like *T. signata* and *T. maculigera* on the same or congeneric host plants. Perhaps, *T. vicina* also provides evidence of a former host transfer from the Helenieae to the Heliantheae (Table 1), or vice-versa.

Resource sharing is practiced by *Trupanea* species at both the host species as well as at the host deme and individual flower head levels in southern California, as noted by Goeden (1985). Zwölfer (1987, 1988) has studied resource sharing among Tephritidae in flower heads of European Cynareae. All species of *Trupanea* for which hosts are known, except probably *T. imperfecta* (Goeden 1988), share some of their hosts with other species of *Trupanea* (Table 2). The number of congeneric species with which hosts are shared varies from a low of one each for *T. californica* and *T. signata*; to two congeners for *T. arizonensis, T. bisetosa, T. conjuncta, T. pseudovicina,* and *T. vicina*; to five congeners for *T. nigricornis* and *T. wheeleri*; to six congeners for *T. femoralis* and *T. radifera*; to seven congeners for *T. jonesi*; to a high of eight congeners for *T. actinobola*. Generally, the stenophagous species share their hosts with the least number of congeners in California (Tables 1 and 2).

Each generalist species of *Trupanea* also shares many of its host species in California, and mainly with one to five other congeneric generalists. *Trupanea actinobola* shares 12 (50%) of its 24 reported host species with congeners; *T. femoralis* similarly shares 24 (71%) of its 34 reported hosts; *T. jonesi* shares 34 (40%) of its 86 reported hosts; *T. nigricornis* shares 38 (63%) of its 60 reported hosts; *T. radifera* shares 15 (43%) of its 35 reported hosts; and *T. wheeleri* shares 22 (73%) of its 30 reported hosts. At least two host species are now known to be shared by all six generalist species in southern California: *Brickellia oblongifolia* Nuttall, an occasional, spring-blooming subshrub in dry, stony places below 2700 m in the tribe Eupatorieae; and *Haplopappus squarrosus* Hooker and Arnott, a common, many stemmed, low, fall-blooming shrub on dry slopes below 1400 m in the tribe Astereae (Munz 1974).

The tribes Astereae, Cichorieae, Heleniae, Heliantheae, and Senecioniae contain the most host-plant genera and species recorded for *Trupanea* flies (Table 1). These tribes

Table 2. Number of host-plant species shared by each of 14 *Trupanea* species with its congeners in California as known to date (see text).

| | *actino-bola* | *ari-zonen-sis* | *bisetosa* | *califor-nica* | *con-juncta* | *femo-ralis* | *imper-fecta* | *jonesi* | *nigri-cornis* | *pseudo-vicina* | *radifera* | *signata* | *vicina* | *wheeleri* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *actinobola* | — | 1 | — | — | 1 | 6 | — | 6 | 8 | 1 | 3 | — | — | 3 |
| *arizonensis* | 1 | — | — | — | 1 | — | — | — | — | — | — | — | — | — |
| *bisetosa* | — | — | — | — | — | 1 | — | 1 | — | — | — | — | — | — |
| *californica* | — | — | — | — | — | — | — | — | — | — | — | 2 | — | — |
| *conjuncta* | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — |
| *femoralis* | 6 | — | 1 | — | — | — | — | 11 | 16 | — | 4 | — | — | 12 |
| *imperfecta* | — | — | — | — | — | — | — | — | — | 1[a] | — | — | — | — |
| *jonesi* | 6 | — | 1 | — | — | 11 | — | — | 19 | — | 10 | — | 1 | 9 |
| *nigricornis* | 8 | — | — | — | — | 16 | — | 19 | — | — | 7 | — | — | 16 |
| *pseudovicina* | 1 | — | — | — | — | — | 1[a] | — | — | — | — | — | — | — |
| *redifera* | 3 | — | — | — | — | 4 | — | 10 | 7 | — | — | — | 1 | 3 |
| *signata* | — | — | — | 2 | — | — | — | — | — | — | — | — | — | — |
| *vicina* | — | — | — | — | — | | — | 1 | — | — | 1 | — | — | — |
| *wheeleri* | 3 | — | — | — | — | 12 | — | 9 | 16 | — | 3 | — | — | — |

[a] See footnote to Table 1.

also are the largest of the total of 12 tribes found in southern California, comprising 22, 23, 25, 30, and seven genera and 117, 61, 65, 89, and 32 species, respectively (Munz and Keck 1959, Munz 1968, 1974).

Several stenophagous species of gall-forming or flower head-infesting Tephritidae have found use in the biological control of weeds (Harris 1989). The dispersed pattern of host-plant incidence depicted in Table 1 also has implications for host-specificity determination of Tephritidae under consideration as candidate agents for biological control. This is because current methods of testing and defining host-plant specificity and safety of use of agents rely principally on a centrifugally arranged array of test plants clustered about the target weed and its most closely taxonomically-allied, cultivated relative, termed a "critical test plant" (Zwölfer and Harris 1971, Wapshere 1974). Away from this central cluster of closely related plants are species representative of other tribes of Asteraceae selected for further definition of the outer limits of the host range of the tephritid. The data in Table 1 suggest that these tribal representatives, often also selected on the basis of availability or ease of culture, probably would not be one of the few host species in those tribes to be attacked by that oligophagous tephritid in nature. These data also demonstrate that hosts of nearly oligophagous, nonfrugivorous tephritids are not necessarily clustered within single tribes of Asteraceae, e.g. *T. vicina*. This is not to denigrate the enviable record that biological control workers have achieved to date in predicting the safety of introduction of phytopagous arthropods (Zwölfer and Harris 1971, Wapshere 1974, Schroeder and Goeden 1986). Rather, these data should simply serve to remind biological control of weed workers that continued caution should be employed, and that overreliance on conventional wisdom that hosts are clustered within taxonomically defined aggregations may be problematic.

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